NUMERICAL TAXONOMY

Robert F. Inger

Field Museum of Natural History

INTRODUCTION

For some strange reason the attitudes of taxonomists and systematists towards the phrase "numerical taxonomy" fall into two extreme positions. On the one hand are those who think numerical taxonomy provides the only means of reaching objective conclusions, that any other approach to taxonomy is sterile, subjective, and really not quite scientific. At the other extreme are those taxonomists who think numerical taxonomy has no place in their science, that it is unclean or is likely to be the death of taxonomy.

The extremists among the numerical taxonomists sometimes leave us with the impression that taxonomists never used statistics prior to 1957. In herpetology statistics as a tool became important with Ruthven's classic study on variation of *Thamnophis* in 1908. The numerical taxonomists often seem to give the numbers more significance than the biological relationships they are ostensibly investigating. Furthermore they also seem to overlook the fact that one cannot increase the objectivity of an observation by assigning it a number.

At the same time we must give the numerical taxonomists their due. One of their major contributions is to stimulate a self-conscious interest in taxonomic methodology. This development has been long overdue. The criticism leveled at traditional taxonomists by the numerical people that our methods are obscure and almost never spelled out is justified. How many taxonomic papers give the philosophical or methodological bases for the decisions reached by the authors? If we do not present our logic, how can a critical reader decide whether our assumptions are justifiable, whether our procedures are correct, and whether our decisions are internally consistent? If a reader cannot evaluate a paper in this way, how can he know whether or not he should accept the conclusions? Surely we do not wish to be in the awkward position of the numerical taxonomists who often find that the only test of their conclusions is agreement with a previously established, traditional classification.

A second contribution of the numerical group is a set of methods designed to facilitate the handling of large masses of data and many taxa. To deal with the relationships of three or four species of *Rana* on the basis of perhaps ten characters is not an overwhelming task. But if the number of taxa goes above 25 and the number of characters over 30, comparison of all possible combinations becomes extremely laborious. A few, not all, of the new computer methods go through the logical processes used by taxonomists. Why should we not take advantage of the speed of the computer and set it to doing certain essential but boring and repetitious tasks?

There is no reason for any taxonomist of quality to fear being replaced by a machine. A computer is really a stupid machine. One instructs it to do something and it will do so endlessly until it receives the proper signal to stop. A computer is a tool, like a microscope. It is not a substitute for a biologist's brain.

There are many steps in taxonomic work that require statistical computations. These are computational problems common in many fields of biology and have no special bearing on taxonomy. We will not discuss them further.

What we are concerned with here are those numerical methods that are specifically designed to deal with the assessment of relationships. This is the very heart of taxonomy and these are the methods we will discuss. Their variety is staggering. Many are outlined in the book by Sokal and Sneath (1963), but many have been developed since. They spring up like mushrooms after a warm rain.

Before going into detail on any of these methods, we should consider several preliminary steps common to many of them. In all numerical methods character analysis is important, as it is in conventional or traditional taxonomy. The kinds of character analysis required by all numerical methods are not identical, but all require that one first determine the states in which a given character occurs in the sample at hand. For qualitative characters these may be present or absent, straight or curved, red or black, or any set of descriptive terms familiar to taxonomists. For quantitative characters the states may be simply the measures, counts, or proportional values observed or some system of grouping the observed values. This step in the procedure clearly is not unique to numerical taxonomy. It is also an essential part of conventional taxonomy when the latter is carried out according to an explicit method.

When a problem involves many taxa and many characters, the tasks of comparing taxa over all characters or characters over all taxa are simplified by coding character states. This is nothing more than assigning numbers to designate the different states of each character. For example, for the character of the pectoral girdle we may have three states, arciferal, transitional, and firmisternal, to which we assign the numbers 0, 1, and 2, respectively. Or we may assign the numbers 0 and 1 to the states absent and present for the character tarsal fold. This is a purely mechanical process, except for one element. For some methods it is important for computational convenience that the coding of states be carried out with their sequential relationship maintained by the code. For example, the states, small, medium, and large, should be assigned numbers that preserve that sequence.

Another essential preliminary step for some of these numerical methods is the determination of direction of change in characters. Without this determination, which of course requires biological understanding, the numerical methods give only phenetic relationships, that is, static relationships based solely on "resemblances existing now in the material at hand" (Sokal and Sneath, 1963, p. 55). Few taxonomists would be satisfied with this essentially non-biological approach.

I will assume that most taxonomists are interested in evolutionary or phylogenetic relationships rather than phenetic ones. If that is indeed our major interest, we will be concerned not only with the common ancestors of taxa, that is, their patristic relations, but also with the branching sequences or cladistic relations of taxa. Hennig (1965) and others have made the point that branching sequences cannot be based on primitive states, which can only show patristic relations. Primitive states may be carried along in haphazard assortment in various lineages and assessment of convergence cannot be based on their distribution. On the contrary, shared derived states define branches or lineages and lend themselves to analysis of the causes of similarity. This is the reason for the importance of determining the direction of change in characters.

The numerical methods fall into two categories based on their objectives. The function of one category is to seek relationships among taxa. The function of the second is to investigate relationships among characters. We will deal here only with the first category and will consider in detail only three of the many types that have been proposed.

SIMPLE PHYLOGENETIC METHOD

The first of these is the simple phylogenetic method (Voris, Ph. D. thesis, U. of Chicago). This method assesses similarity among all possible pairs of taxa, forms clusters of the most similar pairs, and proceeds to form clusters of clusters or of clusters and single taxa.

Similarity is based on all characters examined and is expressed by a variety of coefficients. One coefficient of similarity is based on the ratio of shared states to total characters. In Table 1, the similarity coefficients show clearly the proportion of character states shared by pairs of taxa in this very simple case. The effects of basing similarity coefficients only on shared, derived states may be seen by comparing the two sets of coefficients.

TABLE 1. Similarity coefficients based on ratio of shared states to total characters. Primitive states are underlined.

CHARACTERS:	ASCAPHIDAE	DISCOGLOSSIDAE	PIPIDAE
Tail muscles	present	absent	absent
Ribs	present	present	present
Spiracle	median	median	paired
Adductor longus	absent	absent	absent
Pectoral girdle	arciferal	arciferal	transitional
Presacral vertebrae . .	9	<9	<9

SIMILARITY COEFFICIENTS:	all states	derived states only
Ascaphidae – Discoglossidae	4/6	0/6
Ascaphidae – Pipidae	2/6	0/6
Discoglossidae – Pipidae	4/6	2/6

The simple phylogenetic method starts with similarity coefficients for all possible pairs of taxa in a real problem set. Table 2 shows the complete array of comparisons for frog families. Notice how much lower are the coefficients in the set using only derived states.

The pair with the highest coefficient is selected as the first cluster and the coefficient gives the level of relationship between the members

TABLE 2. Matrix of similarity coefficients of frog families. Data taken from Inger (1967). The coefficients in the upper right half of the matrix are based on all states shared, those in the lower left half on shared derived states only.

					PRIMITIVES IN						
FAMS	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
I. ASCA		.75	.33	.33	.17	.42	.25	.17	.17	.25	.17	.33
II. DISC	.17		.58	.42	.33	.67	.42	.33	.33	.42	.33	.50
III. PIPI	.08	.33		.50	.42	.42	.17	.17	.17	.25	.33	.25
IV. RHIN	.08	.17	.33		.58	.50	.50	.42	.42	.67	.58	.58
V. MICR	0	.17	.33	.50		.50	.58	.67	.67	.67	.67	.67
VI. PELO	0	.25	.25	.33	.42		.75	.67	.67	.75	.67	.83
VII. HYLA	0	.17	.17	.42	.50	.50		.92	.92	.83	.75	.92
VIII. RANA	0	.17	.17	.42	.58	.50	.67		1.00	.75	.75	.83
IX. RHAC	0	.17	.17	.42	.58	.50	.67	.75		.75	.75	.83
X. BUFO	0	.17	.17	.50	.50	.50	.58	.58	.58		.92	.92
XI. ATEL	0	.17	.25	.50	.50	.50	.58	.58	.58	.67		.83
XII. LEPT	0	.17	.17	.42	.50	.50	.58	.58	.58	.58	.58	

PRIMITIVES OUT

of the pair. Since we are interested in obtaining a phylogeny with lineages and their branching sequences defined, we will use only the "Primitives out" half of the chart. Consequently, the highest coefficient is 0.75 which links the Ranidae and Rhacophoridae (VIII and IX in the table). These form our first group.

The next step is to calculate the similarity coefficient of this new group with every other taxa. At this point one has three alternative ways of calculating these new coefficients. These are called single, average, and complete linkage (see Sokal and Sneath, 1963, pp. 180-182) and are illustrated in a simple example (Table 3). The original coefficients connecting each member of a cluster with another taxon (VI in this case) are examined. One may choose the highest coefficient as the level at which to link the third taxon to the group (single linkage), the lowest coefficient (complete linkage), or the average of the coefficients (average linkage).

TABLE 3. Types of linkage in formation of dendrogram based on similarity coefficients.

	Similarity Matrix	Linkage of VI with (VIII – IX)	
		Type	Value
	VI	single	0.42
VIII	0.33	average	0.375
IX	0.42	complete	0.33

In practice most conventional taxonomists use the equivalent of complete linkage —the lowest common ground—. In effect we say that the members of genus so-and-so have at least these characters in common. We will continue the example using complete linkage.

With the new coefficients calculated, the whole array is scanned once more. A new cluster is formed by picking the highest coefficient which may group two previously unlinked taxa or a taxon with our first cluster. This process, which is illustrated in Figure 1, is repeated until all taxa are linked.

From this sequence of grouping and the values used at each linkage step a dendrogram can be prepared (Fig. 2). This dendrogram shows the hierarchy of lineages, the sequence of branching, and an estimate of the maximum evolutionary distance separating taxa. The last is 1.00 minus the similarity level linking the taxa.

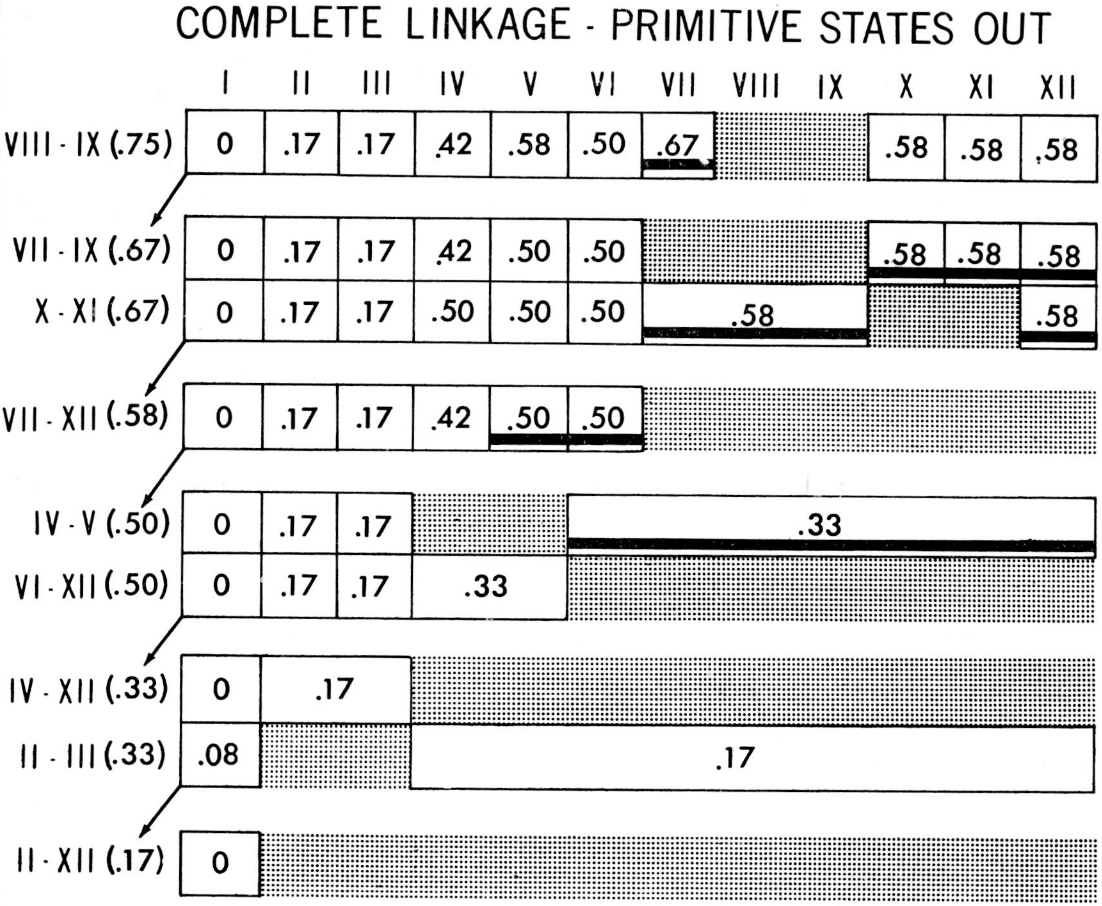

COMPLETE LINKAGE - PRIMITIVE STATES OUT
I II III IV V VI VII VIII IX X XI XII
VIII - IX (.75) 0 .17 .17 .42 .58 .50 .67 .58 .58 .58
VII - IX (.67) 0 .17 .17 .42 .50 .50 .58 .58 .58
X - XI (.67) 0 .17 .17 .50 .50 .50 .58 .58
VII - XII (.58) 0 .17 .17 .42 .50 .50
IV - V (.50) 0 .17 .17 .33
VI - XII (.50) 0 .17 .17 .33
IV - XII (.33) 0 .17
II - III (.33) .08 .17
II - XII (.17) 0

FIGURE 1. Successive formation of clusters of taxa based on similarity coefficients (derived states only) in Table 2 and complete linkage.

To get an idea of the effect of restricting similarity to derived states compare the dendrogram in Figure 2 with another (Fig. 3) based on complete linkage but with primitive states included in the calculations. Note the differences in relationships of the three families on the left and the levels at which the six families on the right are linked.

When the numbers of taxa and characters are large, the calculation of the similarity coefficients and the repeated scanning of the coefficient matrix are tedious operations that do not involve biological understanding or knowledge. These are ideal operations for a computer, which does not be-

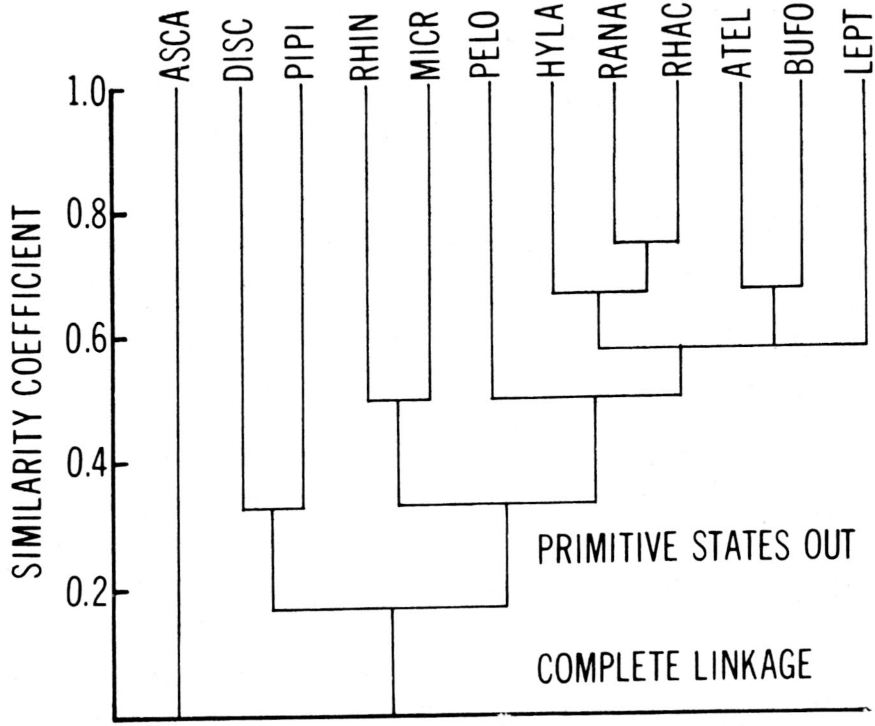


FIGURE 2. Dendrogram of frog families based on similarity coefficients (derived states only) in Table 2 and complete linkage.

come bored no matter how monotonous the task. Computer programs are available that will calculate the coefficients, form the lineages, and print out the dendrogram showing branching sequence and similarity values.

This simple phylogenetic method has several assumptions. In the first place, it assumes that a sampling of the phenotype can give a valid estimate of genotypic similarity. Since we are not likely to have significant amounts of direct information on genotypes of most amphibian species, we will as a matter of practicality be forced to rely on the phenotype. Consequently, this assumption of the simple phylogenetic method must be accepted. We should note that this is a universal working hypothesis applying to all phylogenetic taxonomy.

A second assumption of the simple phylogenetic method, as we have described it, is that all characters are equal, which few taxonomists will accept. Still, this is not fatal to the method, for it is possible to introduce weighting factors into the procedure. One can eliminate characters that, for example, by virtue of excessive intraspecific variation add noise rather than information. Or, following a thorough character analysis, one can restrict calculation of similarity coefficients to genetically independent, significant characters.

The assumptions of this method, therefore, are not a source of weakness. But the nature of the intermediate product, the similarity coefficient, is. Whether the coefficient takes the form of a proportion, a correlation value, a distance measure, or the number of characters shared, the identity of the characters involved in similarity is hidden. There is consequently no way to assess the likelihood of convergence and no immediate way to see which characters have had a history of convergence. Significant correlations among characters are likewise obscured.

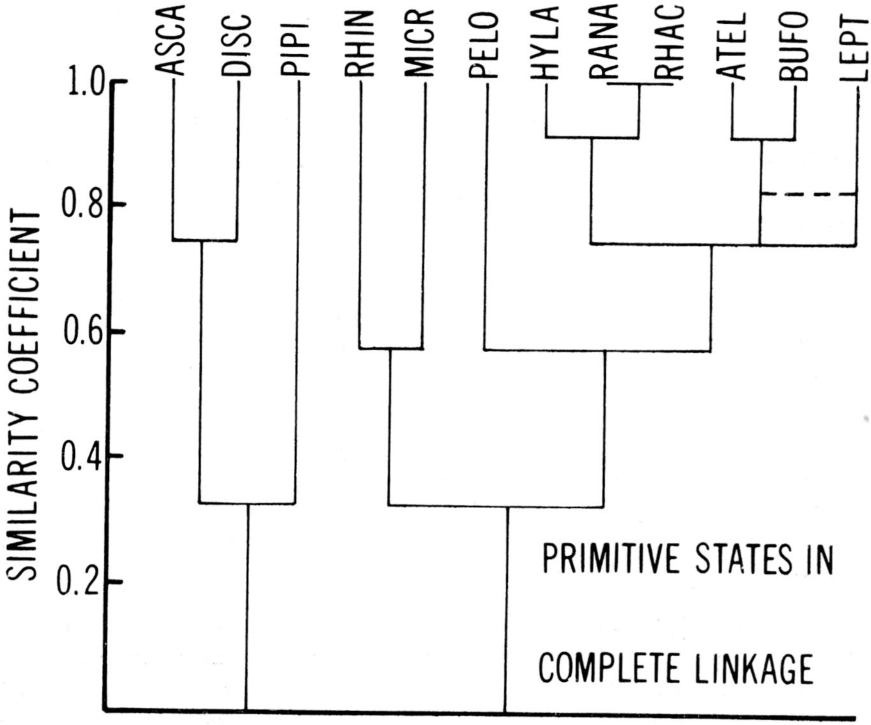


FIGURE 3. Dendrogram of frog families based on similarity coefficients in Table 2, all states included, and complete linkage.

MINIMUM STEPS METHOD

The second method is called the minimum steps method and was devised by Camin and Sokal (1965). Given an array of taxa and character states and given the direction of change of those characters, the method seeks to find the dendrogram that requires the minimum number of evolutionary or mutational steps needed to produce that array.

Starting with a matrix (Table 4) of 12 taxa and 5 characters, we can determine by inspection the minimum number of mutations that must occur to yield the character states. With so few characters and taxa, one can work out several dendrograms (Fig. 4) by trial and error without the help of a computer. However, as the numbers of taxa and characters increase a trial and error approach becomes very burdensome. Camin and Sokal have devised a computer program that will handle up to 30 taxa and 50 characters.

TABLE 4. States of frog families in five hypothetical characters. Total number of states and minimum number of mutational steps required to yield the states given at bottom.

	CHARACTERS				
	1	2	3	4	5
Ascaphidae	0	0	0	0	0
Discoglossidae	1	0	1	0	0
Pipidae	1	1	1	1	0
Rhinophrynidae	1	2	1	0	0
Microhylidae	1	2	1	2	1
Pelobatidae	1	2	1	0	1
Hylidae	1	2	1	0	1
Ranidae	1	2	1	2	1
Rhacophoridae	1	2	1	2	1
Bufonidae	1	2	1	0	1
Atelopodidae	1	2	1	1	1
Leptodactylidae	1	2	1	0	1
States	2	3	2	3	2
Min. Steps	1	2	1	2	1 = 7

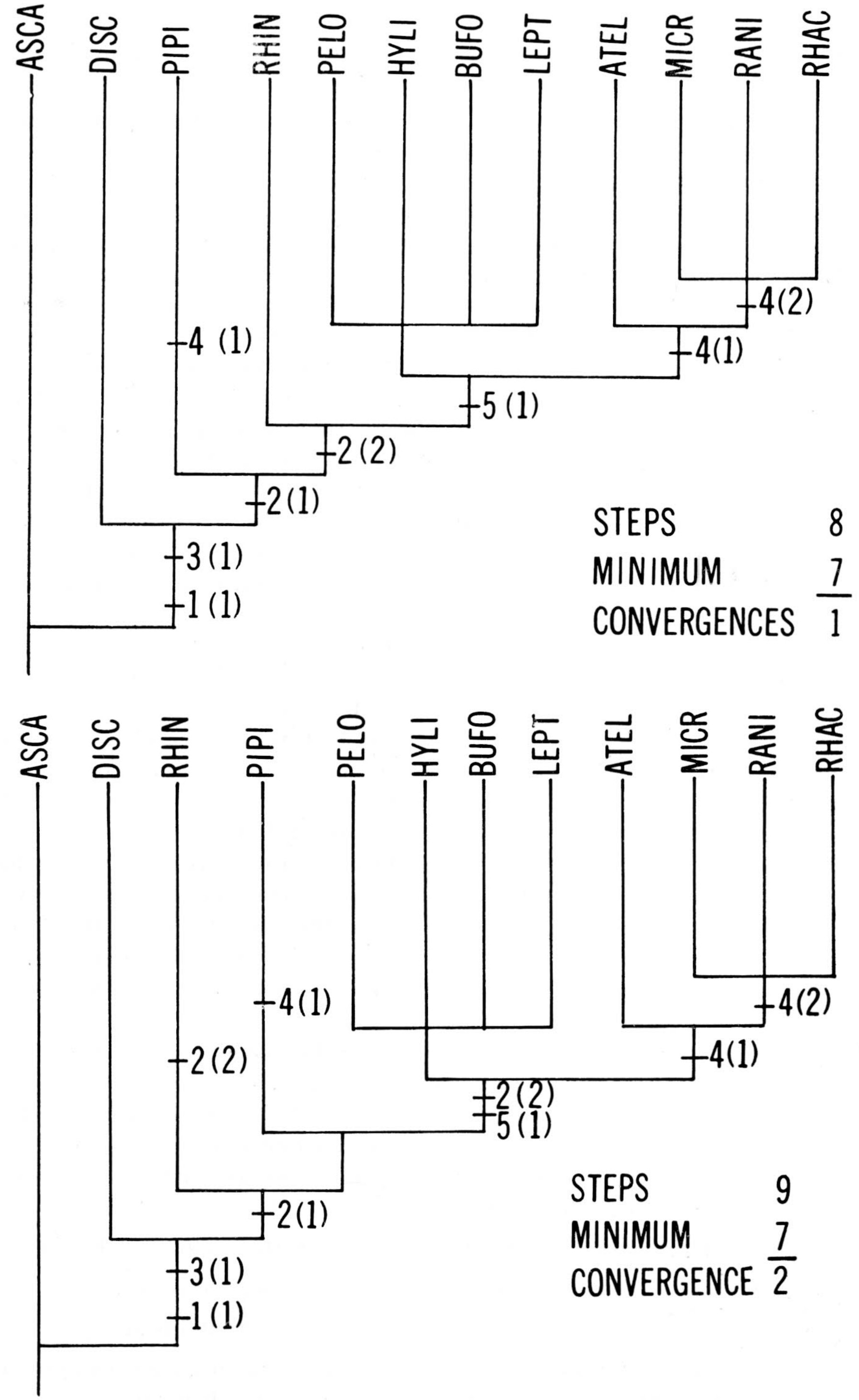

ASCA
DISC
PIPI
RHIN
PELO
HYLI
BUFO
LEPT
ATEL
MICR
RANI
RHAC
4(2)
4 (1)
4(1)
5 (1)
2 (2)
2 (1)
3 (1)
1 (1)
STEPS 8
MINIMUM 7
CONVERGENCES 1
ASCA
DISC
RHIN
PIPI
PELO
HYLI
BUFO
LEPT
ATEL
MICR
RANI
RHAC
4(1)
4(2)
2 (2)
4(1)
2 (2)
5 (1)
2 (1)
3 (1)
1 (1)
STEPS 9
MINIMUM 7
CONVERGENCE 2

Figure 4. Two alternative dendrograms based on the character-taxon matrix of Table 4. The coded states are in parentheses next to corresponding character numbers.

In essence the program works as follows. The computer is instructed to form a trial dendrogram from the data cards, each of which bears the character state data of one taxon. The machine determines how many evolutionary steps are required by that tree. Then it changes the position of one card, forms a new tree, and determines the number of steps or changes implied by the second tree. If the first dendrogram has more steps than the second, the first is eliminated. If the second has more steps, it is eliminated. The machine then changes the position of a different taxon in the tree it has saved in its memory and repeats the process. Each time a taxon is moved the machine determines the number of steps required by the new arrangement, which is saved only if it is more parsimonious, that is, has fewer evolutionary steps than the preceding tree. The computer stops when no new tree is more parsimonious than the one it has retained. The printout gives the dendrogram that is presumably the most parsimonious, that is, the "minimum steps" tree, and the total number of changes in character states required by that tree; the evolutionary steps in each character are marked.

This method has a serious operational limitation. The final, so called parsimonious tree is achieved by a process of successive improvement. If the initial order of the data cards is such that to reach the most parsimonious tree it would be necessary first to increase the number of steps, that is, to pass through a less parsimonious arrangement than the previously saved dendrogram, the machine will not take that move and therefore will not reach the best tree (G. Sharrock, in preparation). Visualize a series of peaks and valleys, the peaks representing relatively parsimonious solutions. The machine is instructed to climb slopes and always move upward. If the order of the data cards starts the machine climbing one of the lesser peaks, the computer can never reach the highest peak if it is separated from the lesser peak by a valley. We have told the machine not to go downhill, and, blindly obedient, it will not.

Consequently, one never knows whether the machine has in fact given us what this method seeks —the minimum steps dendrogram—. A method that is so heavily dependent on a non-biological factor such as the ordering of data cards may not have much appeal to taxonomists.

The minimum steps method has five major assumptions explicitly noted by Camin and Sokal (1965).

1. Discrete character states are definable in the group under study.
2. Character states can be arranged in some logical order.
3. Derived states may arise repeatedly in different lineages.

These three assumptions are part of every evolutionary method in taxonomy, numerical or conventional. I see no escape from them.

4. Evolution is irreversible. A lineage, once it achieves a derived state of a character, cannot return to an ancestral state. A corollary holds that the ancestral state arose just once in the group.

Too much evidence from fossils and contemporary organisms runs contrary to this assumption to permit us to accept it. We need only one example from anurans: the reduction in oral armature in larvae of various genera in scattered families (Inger, 1967).

5. Evolution proceeds in the most parsimonious fashion, always following the path involving the fewest steps and fewest convergences.

This is a proposition that cannot be supported. It implies that all convergences are equally probable, otherwise a dendrogram with a few more steps might be closer to the true phylogeny than the "minimum steps" dendrogram the computer is instructed to produce. In view of differences between characters in morphological and developmental complexity, it is most unlikely that all convergences are equally probable.

This assumption also implies that reversal does not occur.

Thus the minimum steps method, though it starts with data collected following the methods and logic of taxonomy, departs from biological reality in half of its assumptions and has a serious operational handicap that is unrelated to the biological history of any group of organisms.

COMBINATORIAL METHOD

The third of these methods, the combinatorial method (Felsenstein and Sharrock, ms.), is designed to search for nested clusters of taxa grouped on the basis of shared character states. The computer program for this method finds all non-redundant combinations of taxa that share one or more character states. Considering the six taxa in Table 5, we could make a very large number of combinations cantaining from 1 to 6 taxa. Some of these combinations are not monothetic, that is, their members share no states. For example, no combination of A with any other taxon is monothetic. The last five combinations are monothetic; each consists of taxa that share states. But note that combinations BC and CE are both included in a larger group, BCE, sharing the same character states. BC and CE are therefore redundant.

Necessary preliminary steps for the combinatorial program are recognition and coding of states for all characters and taxa, and the determination of direction of change for each character. These are fundamental steps in conventional phylogenetic taxonomy. After these kinds of information are punched on cards the program is run. Felsenstein and Sharrock (ms.) describe the operation in detail. The following is a brief summary. The computer takes one taxon, compares it with all others, reserves those combinations that share at least one state, and notes which states are held in common. Then it takes a second taxon and does the same thing with it, this time making test combinations not only of the second with every single taxon, but also with every monothetic combination formed in the cycle with the first taxon. Then it takes a third taxon and repeats the process of testing combinations for shared states. This procedure is repeated with all taxa, and each time the machine uses another taxon the potential size range of combinations increases by one. Also during this process, the computer eliminates from its memory all combinations that become redundant. Returning to our example, the machine would form group BC and save it until it had formed combination BCE, at which time BC would be eliminated.

With only six taxa and six characters, as in this simple example, the task of forming the combinations is simple for the human eye and hand. No one would resort to a computer. But suppose one were dealing with 40 species of *Bufo* and had data on 25 characters. The number of possible combinations is over 16.000.000 though the number of monothetic combinations in a real problem would be much smaller. Still, the job of finding all of the non-redundant, monothetic combinations would be overwhelming. A large computer could perform this task in less than one minute.

The print-out from the computer includes a list of all non-redundant, monothetic combinations. For each combination the print-out lists the number of states shared, the number of taxa, the serial number of the combination (for convenient reference), the identifications of the taxa by

TABLE 5. Types of combinations based on hypothetical character-taxon matrix. Zero indicates absence, one presence of state.

	States								
Taxa	1	2	3	4	5	6	Taxa	States Shared	Nature of Group
A	0	0	0	0	1	0	AD	none	not monothetic
B	1	1	1	0	0	1	BCE	2, 3	monothetic, non-redundant
C	0	1	1	0	0	0	BC	2, 3	monothetic, redundant
D	0	1	0	1	0	0	CE	2, 3	monothetic, redundant
E	0	1	1	0	0	1	BE	2, 3, 6	monothetic, non-redundant
F	1	0	0	0	0	0	BCDE	2	monothetic, non-redundant

code number, and the identifications of the shared states also in code numbers.

From the print-out the taxonomist selects combinations in such a way that a nested series of clusters results. From the simple set in Table 5, we could make the set of nested clusters or groups shown in the upper part of Figure 5, which would translate into the dendrogram shown on the lower right. During this process, one must make note of the evolutionary or mutational changes. These are indicated in the diagram by the small bars and numbers.

This dendrogram is not the only one possible from the array of taxa and character states. The next illustration (Fig. 6) shows the original dendrogram and an alternative. Other alternatives are possible. The results of changing the relationships among these imaginary taxa are increases in the numbers of evolutionary changes and of convergent states. The small bars and numbers help identify convergences.

There are other technical aspects of the combinatorial method which we need not go into here. They are treated in detail by Felsenstein and Sharrock (ms.).

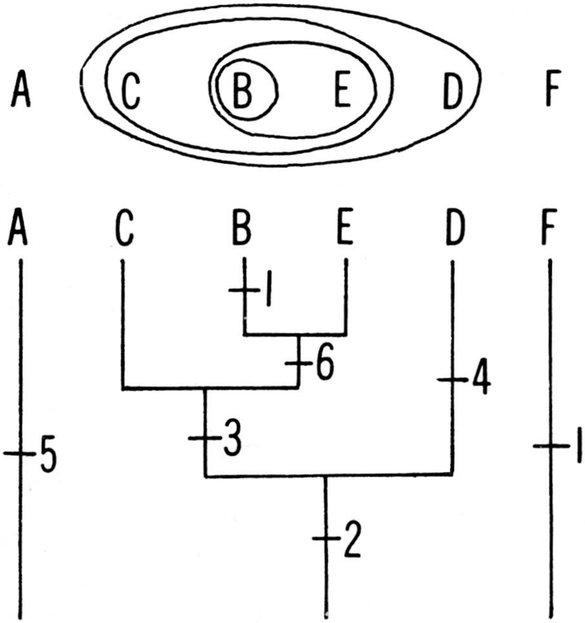


FIGURE 5. Nested clusters (above) and dendrogram based on hypothetical character-taxon matrix of Table 5.

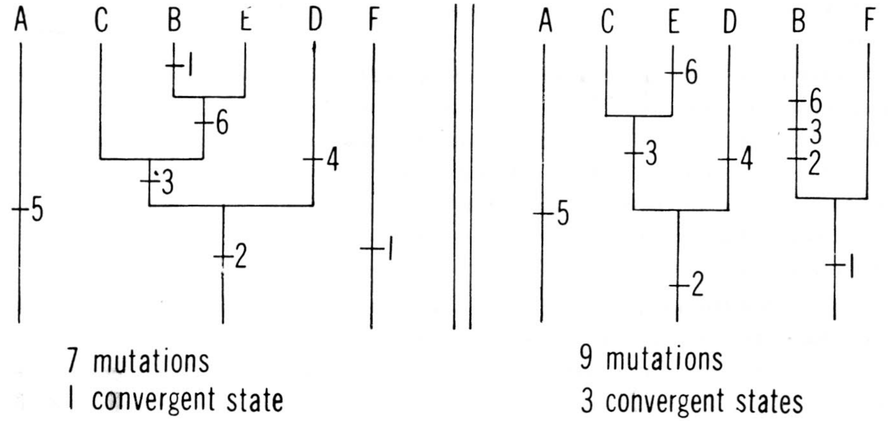


FIGURE 6. Two possible dendrograms based on hypothetical character-taxon matrix of Table 5.

I have applied the combinatorial method to the problem of phylogeny of 12 frog families using 12 characters having a total of 18 derived states. The computer found only 36 non-redundant, monothetic combinations, though the total possible number of combinations is over 1400. A number of dendrograms can be formed from these combinations. Four of them are shown in Figures 7-10.

Since a number of alternative dendrograms can be generated from any set of data, selecting from among them the one that gives the best estimate of the true phylogeny is a major part of the total procedure.

The first step in this stage of analysis is to consider the character states that are involved in convergences in each dendrogram. As we do not believe that the probability for convergence is the same for all character states, scanning the convergent states of the alternative dendrograms may suggest differences in likelihood so gross as to permit restriction of our choice. For example, I doubt that many evolutionists would accept a tree that implied that the vertebrate eye had two independent origins. We simply would not allow convergence in that character.

In comparing the four dendrograms of the frog families (Table 6), one of the derived states least likely to be shared by families as a result of convergence is character state 14, the sinistral spiracle. Dendrograms III and IV, in contrast to I and II, do not require convergence in state 14 and are preferable to I and II. Differences among the other convergent states in terms of probabilities are slight and do not help restrict our choice.

TABLE 6. Comparison of phylogenies of frog families illustrated in Figs. 7-10.

Dendrogram	Number of convergences	Non-convergent states
I	19	1, 4, 8, 9, 16
II	16	1, 2, 4, 8, 12, 16
III	16	2, 11, 12, 14, 16
IV	15	1, 2, 4, 12, 14, 16

Note the differences among these four dendrograms in number of convergences. This brings us back to parsimony as a criterion in choosing among alternatives. If we follow this criterion strictly, our choice is almost automatic and, for reasons we discussed under the minimum steps method, biologically unsound. On the other hand, to ignore this criterion is also perilous. As the number of convergences implicit in a dendrogram increases, the probability that it represents the true phylogeny decreases because convergence in general has a low probability. Confronted with two dendrograms, one having five and the other fifty convergences, we would surely choose the first. The choice is rarely so easy. Usually we have the range of differences seen in our four frog dendrograms: 19, 16, 16 and 15. We considered the first two unlikely on the basis of relative probabilities of convergence of particular states. Hence we are left with III and IV, which differ only slightly in the actual states that converge and by only one convergence. I would hesitate to choose between them.

There are additional ways of evaluating alternative phylogenies. To discuss them let me turn to another problem for which I used the combinatorial method, the relationships among 34 Eurasian forms of *Bufo*, based on 24 derived states (Inger, in press). A data set of this size has approximately 16 million potential combinations. But the computer could find only 133 non-redundant, monothetic combinations. Table 7 compares certain features of four dendrograms formed from this print-out. Let us for the sake of discussion assume that we have examined the convergent states and have found little or no difference between dendrograms in terms of probabilities of their convergences. The trees differ somewhat in total number of convergences. However, I believe the distribution of those convergences shown in the next two columns is more important than the total number.

If we assume that a particular state requires a particular genetic constellation, the more similar the genomes of two taxa the more likely are independent appearances of similar states. From this, it follows that the probability for convergence within major lineages is greater than that for convergence between major lineages, since as part of the logic of taxonomy we try to put more distantly related taxa in separate lineages. The four

TABLE 7. Comparison of four dendrograms relating 34 Eurasian forms of *Bufo*.

Dendrogram	Number of main lineages	Total number of convergences	Convergences within main lineages	Convergences between main lineages	States unique to single main lineages	Main lineages with unique states
I	6	59	21	38	6	3
II	6	56	28	28	10	3
III	3	55	33	22	8	2
IV	3	52	36	16	13	3

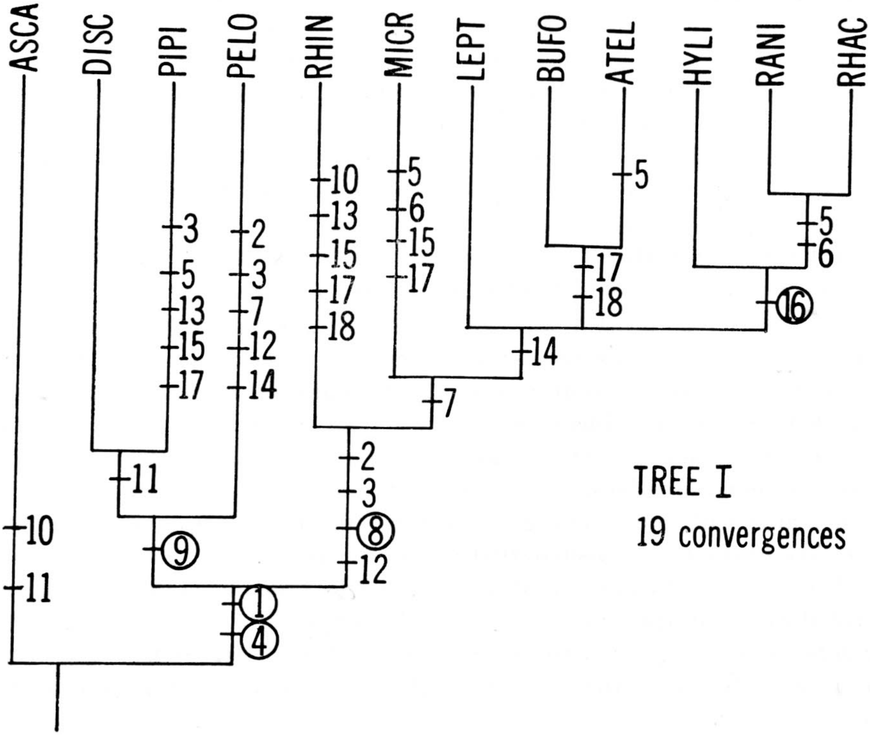

ASCA
DISC
PIPI
PELO
RHIN
MICR
LEPT
BUFO
ATEL
HYLI
RANI
RHAC
10
13
15
17
18
5
6
15
17
5
3
5
13
15
17
2
3
7
12
14
17
18
5
6
⑯
14
7
2
3
⑧
12
11
⑨
10
11
①
④
TREE I
19 convergences

FIGURE 7.

FIGURES 7-10. Alternative relationships of frog families using combinatorial method with 18 derived states. The dendrograms differ in number of convergences and the states involved in those convergences.

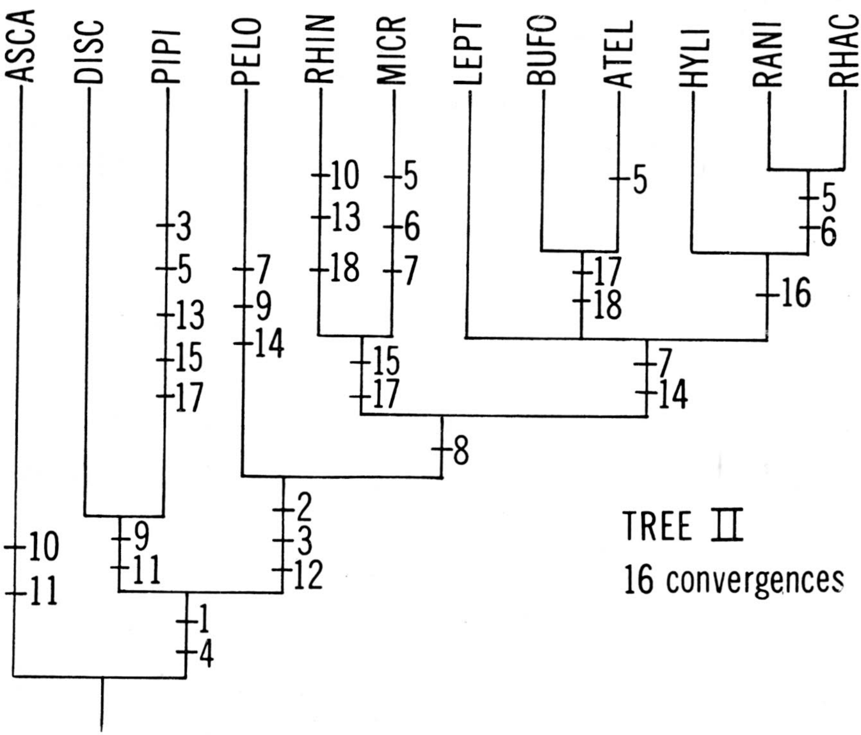

ASCA
DISC
PIPI
PELO
RHIN
MICR
LEPT
BUFO
ATEL
HYLI
RANI
RHAC
10
13
18
5
6
7
5
5
6
3
5
13
15
17
7
9
14
17
18
16
15
17
7
14
8
2
3
12
10
11
9
11
1
4
TREE II
16 convergences

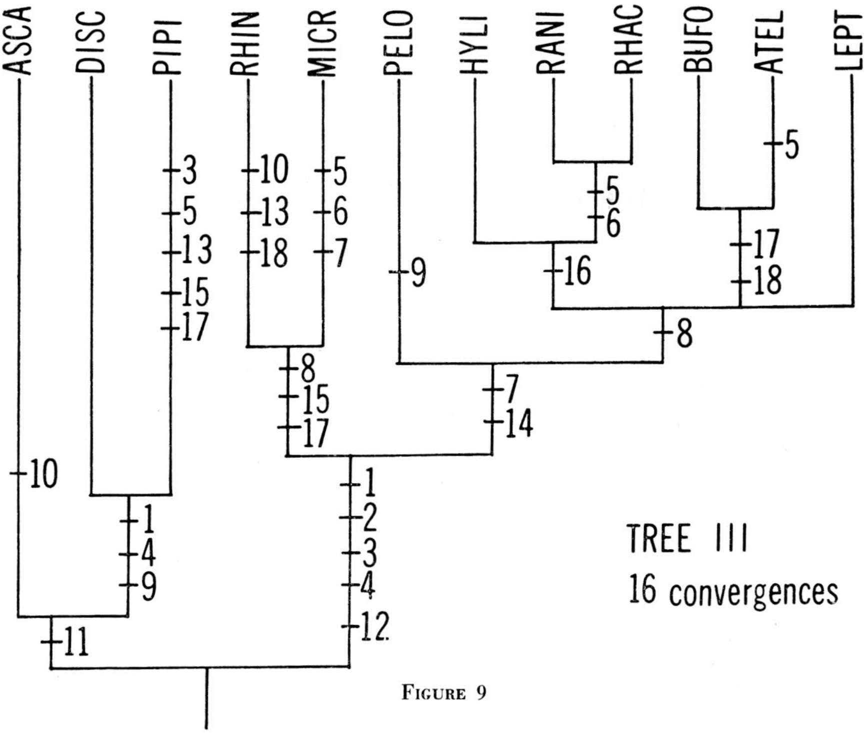
FIGURE 8.

dendrograms are clearly different in this regard, if we compare them in columns 4 and 5. IV is decidedly preferable.

Also as part of the logic of taxonomy we place value on characteristics that are unique to single lineages. The rationale here is that a state confined to one lineage is evidence of genetic distinction for that lineage. The more unique states a lineage has, the more distinct it probably is from other lineages. As taxonomists we prefer our taxa to be distinct from one another. This kind of information is given in the sixth column of the table. Again, the fourth dendrogram is the best.

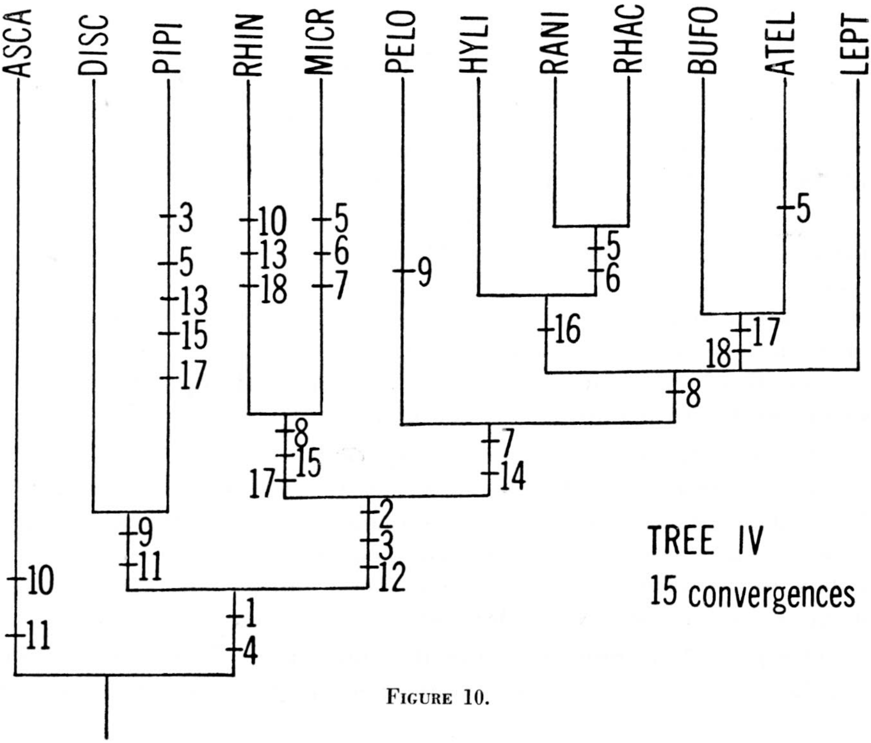
But the total number of states unique to single lineages does not tell us that all lineages are distinct from one another. We need to compare the number of main lineages that have unique states with the total number of main lineages in the dendrogram. Comparing the last column of the table with the second, we see that only in the fourth dendrogram do each of the main branches have at least one unique state.

One part of this process of evaluating alternative dendrograms, estimating the relative probabilities of convergence of the individual states, de-



ASCA
DISC
PIPI
RHIN
MICR
PELO
HYLI
RANI
RHAC
BUFO
ATEL
LEPT
3
5
13
15
17
10
13
18
5
6
7
5
5
6
9
16
17
18
8
8
15
17
7
14
10
1
4
9
1
2
3
4
12
11
TREE III
16 convergences

FIGURE 9



ASCA
DISC
PIPI
RHIN
MICR
PELO
HYLI
RANI
RHAC
BUFO
ATEL
LEPT
3
5
13
15
17
10
13
18
5
6
7
9
5
5
6
16
17
18
8
8
15
17
7
14
9
11
2
3
12
10
11
1
4
TREE IV
15 convergences

FIGURE 10.

pends entirely on understanding and experience with a group. This part of the evaluation cannot be obtained from a computer print-out.

The remainder of the evaluation process depends on information contained in the print-out from the combinatorial method. The criteria used in Table 7 are based on biological reasoning and the numbers resulting from analyzing the print-out give us the basis for an objective ordering of the alternatives.

The computer program obtrudes itself in the process only by eliminating redundant combinations some of which would add to the burden of total convergences. The method has, therefore, an implicit operational feature tending towards parsimony.

The combinatorial is the numerical method for relating taxa that offers the most advantages to taxonomists.

First, it follows the logic of taxonomy in forming trial combinations or clusters of taxa.

Secondly, its assumptions are those forced on all taxonomists: phenotypic similarity is used as a gauge of genotypic relationship; only derived states are used for cladistic relationships; few convergences are preferable to many.

Thirdly, the computer print-out enables the taxonomist to see not only how many states are shared by members of a cluster, but also which states they share. Consequently, at every step in formation of a dendrogram, one can see exactly the evolutionary implications of each tentative relationship.

Fourthly, the print-out contains the kind of information needed to evaluate alternative dendrograms in terms that are both biological in their foundations and quantitative enough to permit objective comparison.

CONCLUSION

The three methods of numerical taxonomy discussed here do not exhaust the variety of such methods, though they represent the major types used for relating taxa. I should like to return to my opening remarks. I believe there is a need to increase the objectivity and clarity of taxonomic methodology. One of the steps in this direction consists of explicit analysis of procedure including the examination of logical consistency and biological validity of underlying assumptions. While we must not equate numbers with objectivity —after all, I could assign numbers to my prejudices— nonetheless, numerical methods may make it possible to compare alternative results in repeatable, quantitative ways. If we can find a numerical method that allows us to test results in quantitative fashion while at the same time exposing the biological implications of those results, we will have taken a big stride towards objectivity and clarity. Of the methods examined here, the combinatorial is by far the most satisfactory in these regards. The other numerical methods either involve unrealistic biological assumptions or do not produce results in a fashion permitting biological evaluation.

ACKNOWLEDGEMENTS

I am indebted to three people, Dr. Lynn Throckmorton and Mr. Glen Sharrock, University of Chicago, and Mr. Harold K. Voris, Yale University, for allowing me to read their manuscripts prior to publication and to incorporate some of their ideas in this paper. However, they should not be held responsible for my interpretations of their ideas.

BIBLIOGRAPHY

CAMIN, J. H. AND R. R. SOKAL
1965 A method for deducing branching sequences in phylogeny. *Evolution, 19:* 311 - 326.

HENNIG, WILLI
1965 Phylogenetic systematics. *Ann. Rev. Entomology, 10:* 97 - 116.

INGER, R. F.
1967 The development of a phylogeny of frogs. *Evolution, 21:* 369 - 384.

RUTHVEN, A. G.
1908 Variations and genetic relationships of the garter snakes: genus *Thamnophis. U. S. Nat. Mus. Bull. 61,* pp. 1 - 201.

SOKAL, R. R. AND P. H. A. SNEATH
1963 Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco, 359 pp.